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Termite Mounds House a Diversity of Taxa in Oil Palm Plantations Irrespective of Understory Management

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ABSTRACT

We investigated the effects of oil palm understory vegetation management on termite mound activity and non-termite inhabitants. We found a diversity of taxa, most of which were unaffected by understory management. Mound volume and termite activity had taxa-specific effects on abundance. Preserving mounds in oil palm plantations will benefit biodiversity.

ABSTRACT IN INDONESIAN

Kami menyelidiki efek manajemen vegetasi lantai di perkebunan kelapa sawit terhadap aktivitas rayap dan penghuni selain rayap dalam gundukan. Kami menemukan beragam taksa, yang sebagian besar tidak terpengaruh oleh manajemen vegetasi lantai. Volume gundukan dan aktivitas rayap memiliki efek taksa spesifik terhadap kelimpahan. Mempertahankan gundukan di perkebunan kelapa sawit akan menguntungkan biodiversitas.

DATA AVAILABILITY STATEMENT

The data used in this study are archived at the Dryad Digital Repository (DOI: 10.5061/dryad.b2rbnzs9g).

KEY WORDS

Elaeis guineensis, habitat heterogeneity, herbicide, Indonesia, Macrotermitinae, *Macrotermes gilvus*, termitaria, termitophile

TEXT

The global demand for palm oil and resultant expansion of oil palm plantations are primary drivers of deforestation (Wicke *et al.* 2011) and biodiversity loss (Foster *et al.* 2011) in South East Asia. Sustainable management of monoculture crops that encourages biodiversity is therefore an important priority, highlighted by certification schemes such as the Roundtable on Sustainable Palm Oil (RSPO). Habitat complexity increases the abundance of microhabitats which in turn supports a higher diversity of organisms (Benton *et al.* 2003, Bennett *et al.* 2006, Seibold *et al.* 2016). In oil palm plantations, habitat complexity has been implemented by preserving forest patches, preserving and creating riparian buffers, and by enhancing understory vegetation (Lucey *et al.* 2014, Luke *et al.* 2018). The latter can grow up to several metres tall in mature oil palm plantations (Tan *et al.* 2014), and studies have shown that maintaining understory vegetation encourages plant, invertebrate and vertebrate biodiversity (Ashton-Butt *et al.* 2018, Hood *et al.* 2019, Luke, Purnomo, *et al.* 2019). Despite this, liberal use of herbicides which reduce, or altogether remove, the understory is common practice, with herbicides accounting for more than 90 percent of a typical plantation's pesticide inputs (Page & Lord 2006).

Termites are ecosystem engineers that contribute to habitat resilience by reducing the effects of drought (Ashton *et al.* 2019) and promoting primary productivity (Jouquet *et al.* 2011). By doing so, termites promote biodiversity in the surrounding area too; for instance, termite mounds have been shown to support a diversity of animal species by acting as resting or nesting sites. Taxa associated with termite mounds include birds (Vasconcelos *et al.* 2015), mammals (Valdivia-Hoeflich *et al.* 2005), snakes (Riley *et al.* 1985, Moreira *et al.* 2009), lizards (Vitt *et al.* 2007), and invertebrates (De Visser *et al.* 2008).

Termite diversity is limited in oil palm plantations due to their sensitivity to environmental variability, however, species of the fungus-growing Macrotermitinae that create protective mounds that buffer against habitat disturbance are relatively common (Lavelle *et al.* 2014, Luke *et al.* 2014). Although the presence of termites in oil palm plantations is valuable for soil moisture retention and nutrient cycling (Foster *et al.* 2011), mounds are often removed to ease harvesting access or because termites are mistakenly identified as pest species (Corley & Tinker 2016).

In this study we investigate the effect of oil palm understory management on termite mound activity and the use of termite mounds by non-termite inhabitants, including their nest site preferences. We predict that plots with more understory vegetation will have a higher proportion of active mounds due to greater understory biomass, a food resource for fungus-growing termites (Luke, Purnomo, *et al.* 2019). Additionally, since changes in understory management affect invertebrates and vertebrates (Ashton-Butt *et al.* 2018, Hood *et al.* 2019), we expect changes in non-termite inhabitants too.

Fieldwork was conducted in Sumatra, Indonesia (0° 56′0” N, 101°18′0” E, 10 – 30 m a.s.l.) in oil palm plantations which are part of the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Programme. The site was converted to oil palm from logged lowland rainforest between 1985 – 1995 and the climate has an average temperature and rainfall of 26.8°C and 2400 mm respectively. Across the plantation, oil palm has been planted in staggered rows at a density of 147 palms/ha.

Three experimental understory management treatments were established in February 2014:

1. **Reduced** complexity where all understory vegetation was removed using herbicides.
2. **Normal** complexity where the management did not diverge from standard industry practice at the site. This included herbicide spraying of vegetation in harvesting paths

and circles (1.5 m radius around the base of each tree). Large woody vegetation was removed manually.

3. **Enhanced** complexity where the understory vegetation in the harvesting paths and circles was cleared manually using a strimmer. No herbicide was employed in this treatment, and large woody vegetation was removed manually.

The treatment plots were each 150 m x 150 m and assigned in a randomised complete block design with four replicates. Plots within blocks were 150 m apart and the blocks were at least one kilometre apart (see Luke, Advento, *et al.* 2019 for full information on study site and experimental design).

We surveyed the centre of each plot (subplot: 66 m × 66 m) between April – May 2018 (only three normal plots were sampled). We measured mound height and radius, and by destructively searching 85 percent of the aboveground volume of each mound (Figure S1), we sampled mound activity (living or dead mounds) and the presence of any non-termite inhabitants. This destructive sampling did not cause any additional adverse impact on the environment as the plots were due to be replanted. Snakes and spiders were photographed in the field and identified to family (and species when possible) using taxonomic keys (Brown *et al.* 1999, Keogh *et al.* 2001, Dippenaar-Schoeman & Jocqué 2007, De Lang 2017, World Spider Catalog 2017) (Figure S2). We recorded ant nests in the termite mounds of which two common genera (*Odontomachus* and *Anoplolepis* (species *Anoplolepis gracilipes*)) were identifiable in the field, while all other ant genera were classified as "other". Termites were identified using the key to termite species by Thapa (1981).

Only eight termite mounds were encountered across the three normal plots compared with 25 in the four enhanced plots and 31 in the four reduced plots. This variation was due to initial patchiness before the vegetation treatments were applied (personal observation). Due to the small sample size in the normal plots, we removed these from the analysis. We ran

generalized linear mixed models (GLMM) in R (version 3.5.1) to determine the impact of understory management (enhanced and reduced) and mound size on termite mound activity, and ran further GLMMs with these three variables as predictors against the abundance of the most common non-termite inhabitants (ants, snakes, spiders, and centipedes) (Supplementary Material 1). Mound preference of snake families, spider families, and ant genera were analysed in relation to the treatments using two-tailed Fisher's Exact Tests (Ruxton & Neuhäuser 2010).

We encountered one mound-building termite species, the fungus-growing *Macrotermes gilvus*. Across the treatment plots (reduced and enhanced) the termite mounds had an average volume and density of 5.4±3.4m^3 and 16.4±4.7/ha respectively, and 57 percent of mounds were active. The four most commonly encountered taxa were snakes (44 individuals, 11 nests), spiders (39 individuals, 6 nests), centipedes (71 individuals), and ants (48 nests). Snake species *Ramphotyphlops lineatus* (Lined Blind Snake), *Pseudorabdion longiceps* (Dwarf Reed Snake), and *Naja sumatrana* (Equatorial Spitting Cobra) were found nesting with eggs in the mounds, and *Python brongersmai* (Brongersma's Short-Tailed Python) was found resting. Scorpions, beetles, cockroaches, and earthworms were also encountered, but these were too rare to be included in the analysis.

Model comparison (using AIC, Supplementary Material 1) indicated that vegetation treatment did not impact mound activity or the total abundance of the four most common inhabitants, and it was removed from the final models. Mound volume did not impact mound activity either, and it was removed, and the null model was chosen. Mound volume and activity did impact total non-termite inhabitant abundance. Snake abundance increased with mound volume but decreased with mound activity, while ant nest abundance decreased with mound volume (Figure 1, Table S1). Neither mound activity nor volume had a significant impact on spiders. Mound activity was included in the final model for centipede abundance,

but its effect was not significant (Figure 1, Table S1). Although the treatments did not impact the total abundance of the most common groups, the composition of snake families (P = 0.005, Fisher's exact test) and ant genera (P = 0.016, Fisher's exact test) were affected by the treatments, with more Colubridae and fewer Typhlopidae and *Anopololepis* in the enhanced than the reduced plots (Figure 2). The composition of spider families was not affected by the treatments (P = 0.420, Fisher's exact test, Figure 2).

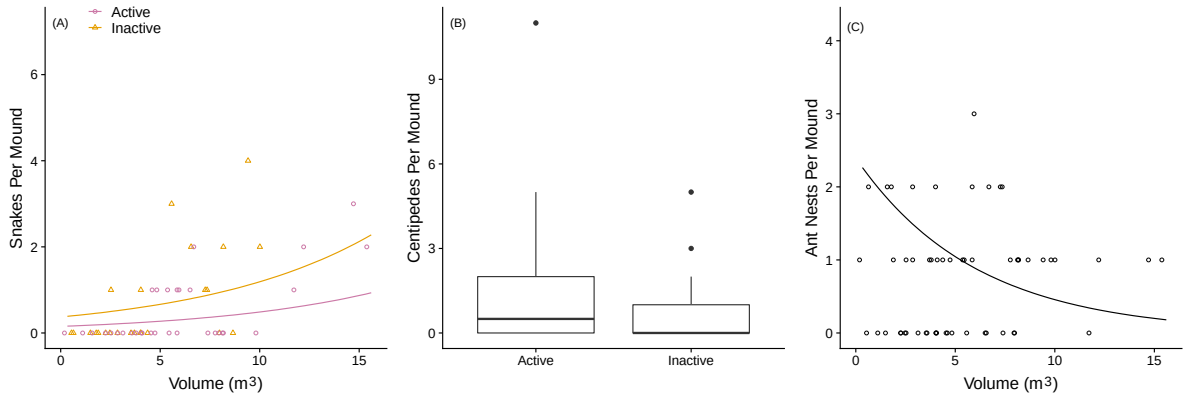

FIGURE 1. The abundance per mound of: (A) snakes by volume for active and inactive mounds; (B) centipedes by mound activity; and (C) ant nests by volume. Shaded areas show 95 percent confidence intervals around lines of best fit (Supplementary Information 1). Each point shows a single termite mound. Although there was a trend for increased centipede abundance in active mounds (B, P=0.06), this relationship was not significant when an outlier was removed (P=0.57, see Table S1).

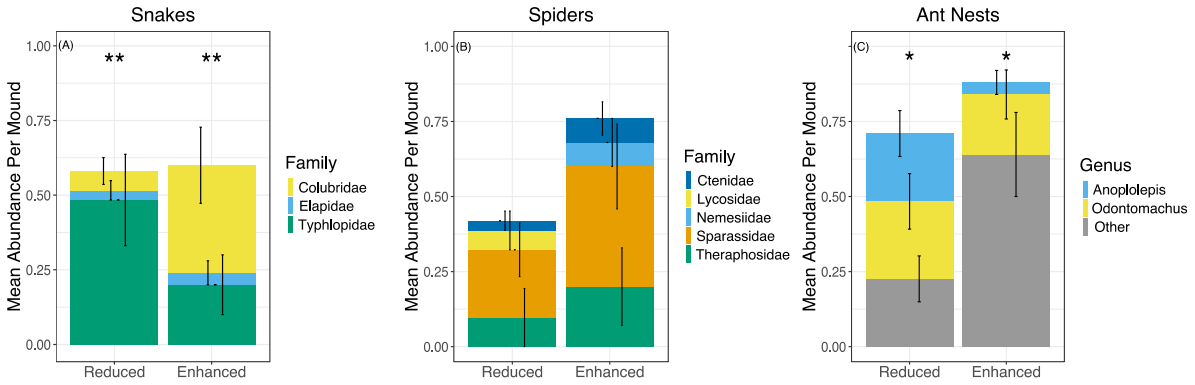

FIGURE 2. Mean abundance per mound of: (A) snake families; (B) spider families; and (C) ant nests (sorted to genera and including group "Other" for those that were not identified) by vegetation treatment (reduced and enhanced). Asterisks show significant differences in group composition, according to Fisher's Exact tests. Significance codes are: P<0.01**, P<0.05*. Error bars show standard error.

The mound building termite *M. gilvus* was the sole contributor to the mounds in the study site. It belongs to the most commonly encountered termite subfamily (Macrotermitinae) in oil palm plantations in South East Asia (Luke *et al.* 2014, Wong *et al.* 2016). Understory vegetation management did not impact the activity of termite mounds in the plantation, suggesting that *M. gilvus* is highly resilient to anthropogenic disturbance, habitat simplification and resource removal. There was also little impact of vegetation removal on non-termite mound inhabitants, indicating that termite mounds provide important nesting sites in different habitats. As abundances of species outside the mounds were not examined, we are unable to comment on the preference of termite mounds as nesting sites compared with other microhabitats. However, this study supports previous work that has found termite mounds act as refuges for a range of animals (Choosai *et al.* 2009, Joseph *et al.* 2013, 2015).

It is also noteworthy that the abundance and diversity of snakes in the termite mounds was surprisingly high. While snakes have been found to rest in termite mounds (Angelici *et*

al. 2000, Duleba & Ferreira 2014) evidence of nesting within mounds is scarce (but see Riley *et al.* 1985). To our knowledge, this is the first example of Elapidae and Pythonidae using mounds in this manner. Benefits of nesting in mounds include protection against predators (Brightsmith 2000), microbes or parasites (Kalko *et al.* 2006), the provision of a stable environment (King *et al.* 2017) (which is particularly important for egg development (Knapp & Owens 2008)), and food for insectivorous species (Vitt *et al.* 2007). However, as fewer snakes were recorded in active mounds, the latter benefit was most likely not a primary driver of nest site selection. The increase in snake abundance in larger mounds, on the other hand, suggests that microclimatic protection was an important driver, as larger mounds buffer temperature more effectively (Vesala *et al.* 2019). Preference for larger termite nests has been observed in other taxa too, such as birds (Brightsmith 2000).

In contrast to snakes, the abundance of ant nests was higher in small termite mounds. This may be due to the selection of warmer habitats by ants, as smaller termite mounds tend to have poorer heat regulation (Vesala *et al.* 2019). Additionally, termite predation by ants is widespread (Prestwich 1984, Berghoff *et al.* 2002) and termites are therefore expected to be on high alert regarding ant intrusion. As larger termite mounds comprise a higher number of individuals, they may reduce the success of nest establishment due to better defence. Neither centipedes nor spiders were affected by termite mound activity or size, suggesting that their presence in the mounds may not trigger a termite response.

Our results suggest that termite mounds are resilient to habitat disturbance and resource removal and that they provide suitable nesting sites for animals in oil palm plantations. Without better understanding of the abundance of non-termite mound inhabitants in the surrounding habitat, we are unable to quantify the importance of termite mounds as nesting sites. However, we suggest that the removal of understory vegetation provides fewer microhabitats and therefore a reduced number of nesting spots compared with areas where

vegetation is allowed to grow. It is therefore likely that the presence of termite mounds in simplified habitats provide shelter for a larger proportion of the overall biodiversity. This possibility should be tested.

While the resilience of termite mounds allows for animals to take advantage of them regardless of habitat management, mounds are often removed during harvest and plantation replanting. As millions of hectares of oil palm plantations are now due to be replanted (Snaddon *et al.* 2013), we must urgently determine the vulnerability of termites and their mounds to the replanting process in oil palm plantations. The current replanting process involves clearing vast swathes of land, resulting in hectares of homogenous exposed soil and subsequent biodiversity loss (Kurz *et al.* 2016, Ashton-Butt *et al.* 2019). Actively retaining a range of mound sizes through this process will provide an important habitat for species. Efforts should be made to improve understanding amongst plantation managers and workers of the value of mound-building termites in plantations. This will allow for better identification of pest species (Corley & Tinker 2016) and enable termite mounds to be actively conserved during management operations to maintain potential associated benefits to decomposition (Foster *et al.* 2011), soil stability and biodiversity.

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AUTHOR CONTRIBUTION STATEMENT

AH and ET conceived the study. AH, ADA and AAKA collected the data, with input from ET, JP and MN on study design. MP, CD and JH identified the animals. AH wrote the original draft, and all authors reviewed and edited it.

CONFLICT OF INTEREST

Co-authors listed with a Sinar Mas Agro Resources and Technology Research Institute (SMARTRI) affiliation were employed by SMARTRI, the research division of Golden Agri Resources (GAR), at the time of the study. The wider BEFTA Programme is co-funded by GAR. However, there is an MOU in place that protects the intellectual freedom and data-use for all researchers working on the project. The Programme therefore represents a collaboration between the University of Cambridge and an oil palm company, ensuring that results are readily disseminated to inform best management practices, but maintaining academic independence.

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SUPPLEMENTARY INFORMATION

Supplementary Information 1. Shows the specifics of the two models and their outputs. For Eqn 1 we used a binomial distribution and a logit link as the data were binary. For Eqn 2 we used a Poisson distribution and a log link as the data were in counts. We included the random effect Plot, but not Block as it would have only had four levels. For Eqn 2 we included an offset of the logarithm of mound volume to convert abundance per mound to density per volume sampled. Therefore, dependent variables were density of the most common groups. Data exploration was conducted following Zuur *et. al.* 2010, and model construction and validation were conducted following Zuur & Ieno 2016. We simplified the models by selecting those with the lowest Akaike's Information Criterion (AIC). Where $\Delta < 2$, we applied the nesting rule, and discarded models that were more complicated versions of those that had a lower AIC value (Richards *et. al.* 2011). We simplified all models, even those with single predictors, by comparing them to intercept-only models. When modelling centipede density, we found that one of the points was highly influential (Cook's distance > 1), so we removed this point and reran the analysis. We used R Studio version 1.0.153 (RStudio Team 2016) with packages tidyverse (Wickham 2017) and cowplot (Wilke 2019) for data wrangling and plotting, and packages influence.ME (Nieuwenhuis *et. al.* 2012), lme4 (Bates *et. al.* 2015), and glmmTMB (Brookes *et. al.* 2017) for constructing and validating models.

$Activity_{ij} \sim Binomial\ (\pi_{ij}, N_{ij}, \phi)$

$E(Activity_{ij}) = \pi_{ij} * N_{ij}$

$Var(Activity_{ij}) = \pi_{ij} * N_{ij} * (1 - \pi_{ij})$

$logit(P_{ij}) = Understory_{ij} + Plot_{i}$

Where:

$Activity_{ij}$ (mound activity: categorical, 2 levels) is the *j*th observation in plot *I*, and *J* = 1,. . ., 56

$Plot_i$ is the random intercept, and *I* = 1,. . ., 11

Understory is understory vegetation treatment: categorical, 2 levels (eqn 1)

$Abundance_{ij} \sim Poisson(\mu_{ij})$

$E(Abundance_{ij}) = \mu_{ij}$

$Var(Abundance_{ij}) = \mu_{ij}$

$\log(\mu_{ij}) = Understory_{ij} + Activity_{ij} + Volume_{ij} + offset(Volume)_{ij} + Plot_i$

Where:

$Abundance_{ij}$ (abundance of spiders, ant nests, centipedes or snakes: continuous) is the *j*th observation in plot *I*, and *J* = 1,. . ., 56

$Plot_i$ is the random intercept, and *I* = 1,. . ., 11

Understory is understory vegetation treatment: categorical, 2 levels

Activity is mound activity: categorical, 2 levels

Volume is volume of soil searched: continuous (eqn 2)

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Table S1. Estimated regression parameters, standard errors, *z*-values and *P*-values for the Poisson GLMMs presented in Eqn2 above. These are the simplified models, all initial models looked at the effect of vegetation treatment, mound volume, and activity on the four most abundant groups (snakes, spiders, centipedes and ants). All predictors were removed for the spider model. Two models are shown for centipede abundance, as the results differed when an

influential outlier was removed. Significance codes are: P<0.001***, P<0.01**, P<0.05*, P<0.1'.

Group	σ_{Plot}		Estimate	Std. error	*Z* value	*P*-value
Snakes	$3x10^{-9}$	Intercept	-2.94	0.36	-8.29	<0.001***
		Volume[1]	0.39	0.17	2.25	0.024*
		Active	-0.89	0.38	-2.34	0.020**
Centipedes	0.133	Intercept	-1.46	0.21	-7.08	<0.001***
		Active	0.57	0.30	1.88	0.060'
Centipedes:	0.032	Intercept	-1.67	0.19	-9.02	<0.001***
No Outlier		Active	0.17	0.30	0.57	0.567
Ants	$8x10^{-9}$	Intercept	-1.71	0.15	-11.26	<0.001***
		Volume[1]	-0.56	0.17	-3.25	0.001**

[1]Volume = Standardised Mound Volume

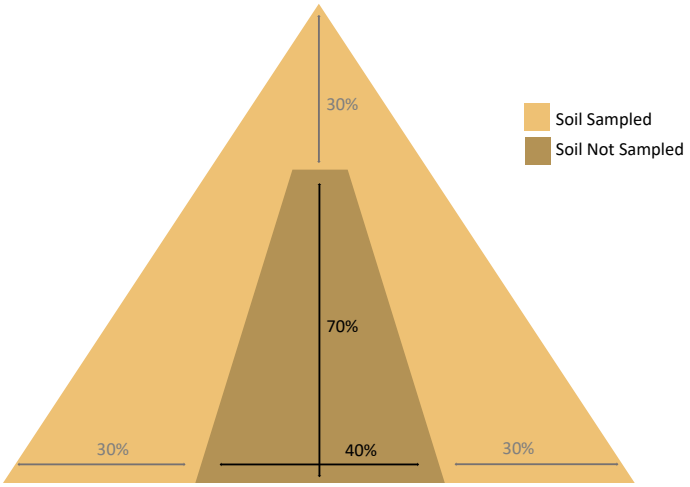

Figure S1. Diagram showing the proportion of each termite mound that was manually searched. We removed the outer and upper 30 percent of each mound. Assuming that the mounds were cones (i.e. their volume was π*radius^2*height/3), the soil sampled amounted to 85 percent of the total volume of the mound.

Figure S2. Photos of spiders from family: (A) Theraphosidae with egg sack; (B) Theraphosidae; (C) Nemesiidae; (D) Sparassidae; and (E) Sparassidae. Photos of snake species: (F) *Ramphotyphlops lineatus*; (G) *Pseudorabdion longiceps*; (H) *Python* Cf. *brongersmai*; and a (I) *Naja sumatrana* nest.